

On the Anatomy and Fine-Structure of a Peculiar Sense Organ in *Nucula* (Bivalvia, Protobranchia)

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Abstract. A peculiar, tubelike sense organ, called Stempel's Organ (StO) is found in the protobranch genus *Nucula* immediately dorsal to the anterior adductor muscle. The single organ forms a closed tube which is cerebrally innervated. So-called collar receptors present in the sensory portion of the StO indicate a mechanoreceptive function of the organ. Three special muscles are attached to the StO: two of them (m2 and m3) stabilize the tube, the third (m1), whose contractions are detected by the organ, is used in connection with the special mode of feeding (by palps, palp proboscides, and ctenidia) found in the Nuculidae. Comparison is made between the StO and other molluscan sense organs, likewise having collar receptors.

INTRODUCTION

AT THE END OF THE last century, STEMPELL (1898) described a peculiar, tubelike organ in *Nucula nucleus*, located dorsally to the anterior adductor muscle. Although he investigated its histology in some detail, the author could not trace any special function of the suggested sense organ. Later on, this organ was noticed by DREW (1901) in his admirable paper on the ontogeny of *Nucula delphinodonta*. According to the author this "organ of unknown function" appears during embryogenesis together with the first anlage of the ctenidium, a short time after the test of the embryo is shed. Since that time this peculiar sense organ has not been reported by scientists.

In honor of its discoverer I shall call this structure Stempel's Organ (StO). In this paper a detailed description of the anatomy and the fine-structure of the StO will be presented with a discussion on its presumed function.

MATERIAL AND METHODS

Nucula nucleus (Linné, 1758) and *Nucula sulcata* (Bronn, 1831), both from the Atlantic (Bergen, Norway), were histologically and fine-structurally investigated with respect to the StO.

For histological investigations serial sections were used, stained with Heidenhain's Azan.

For ultrastructural research entire specimens (3-5 mm) of *Nucula nucleus* were fixed in phosphate-buffered glutaraldehyde (2.5%) and osmium (2%), decalcified with ascorbic acid (1%) after DIETRICH & FONTAINE (1975), and embedded in an epon-araldite mixture (MOLLENHAUER, 1964). Semithin sections were stained with 0.1% toluidine-

blue, while ultrathin sections, made with a diamond knife, were stained with uranyl acetate and lead citrate. For observation a Zeiss EM9/S2 was used.

RESULTS

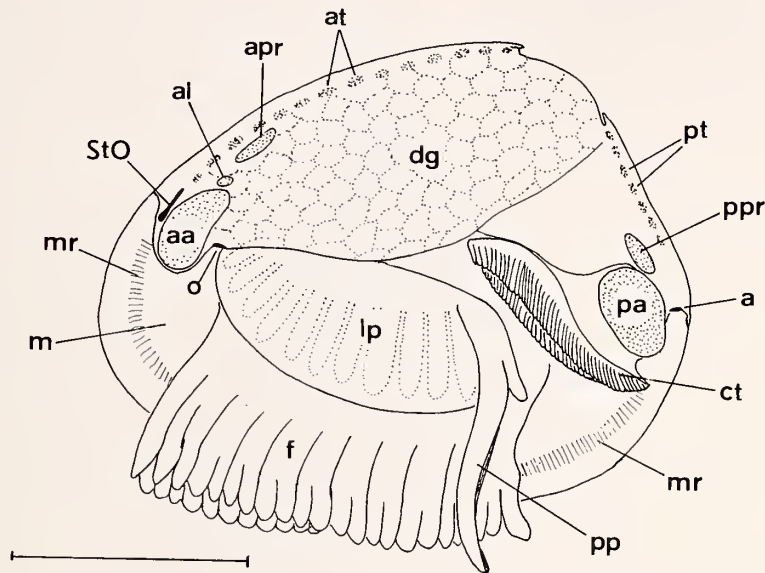
Anatomical Context of Stempel's Organ

Position and innervation: The StO is located dorsal to the anterior adductor (Figures 1, 2). There is some variation with respect to the position of the posterior end of the StO, which may reach the first tooth of the hinge or a little into the dorsal mantle process. The organ forms a narrow, elongate tube nearly as long as the anterior adductor in adult specimens 700-800 μm , closed at both ends. Its diameter varies between 30 and 60 μm , depending on the state of contraction of the attached muscles (see below). The anterior end of the StO is always expanded and forms a bulb (see DREW, 1901, and Figure 1b).

Innervation is from the pair of anterior pallial nerves which emerge from the outside of the most dorsal/anterior parts of the cerebral ganglia (Figure 1b).¹ Each nerve runs

¹ In this respect it should be stressed that the pleural ganglia of *Nucula* (*N. nucleus*, *N. sulcata* investigated here, *N. delphinodonta* after DREW, 1901) are not separated as described by PEL-SENEER (1891), but are fused as in all other bivalves. In addition, the visceral loop is not a nerve, but a neural cord over its whole length, as known from the primitive cephalopod *Nautilus*. Since neural cords in primitive gastropods are pedal ones, evolution of ganglia in higher conchiferous groups is clearly due to convergence, contradicting a (monophyletic) taxon "Ganglioneura" (LAUTERBACH, 1984).

1a



1b

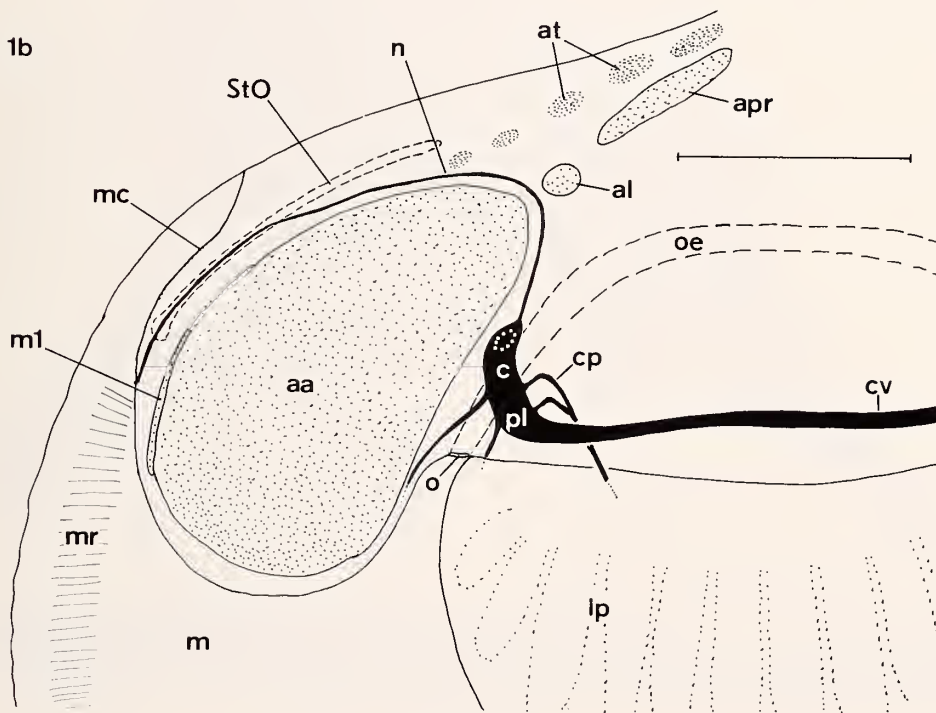


Figure 1

Nucula sulcata. Position and innervation of Stempell's Organ (StO). Figure 1a, lateral view of the left side (left mantle omitted). Figure 1b, detail view to show innervation of the StO (all tissues are shown transparent). a, anus; aa, anterior adductor; al, anterior retractor of labial palp; apr, anterior pedal retractor; at, anterior teeth of hinge; c, cerebral ganglion; cp, cerebro-pedal connective; ct, ctenidium; cv, cerebrovisceral connective; dg, digestive gland; f, foot; lp, labial palp; m, mantle; m1, attachment zone of muscle m1; mc, central cleft of mantle margin; mr, mantle retractors; n, nerve of StO; o, oral opening; oe, oesophagus; pa, posterior adductor; pl, pleural ganglion; pp, palp proboscides; ppr, posterior pedal retractor; pt, posterior teeth of hinge; StO, Stempell's Organ. Scale bars: 1a, 5 mm; 1b, 1 mm.

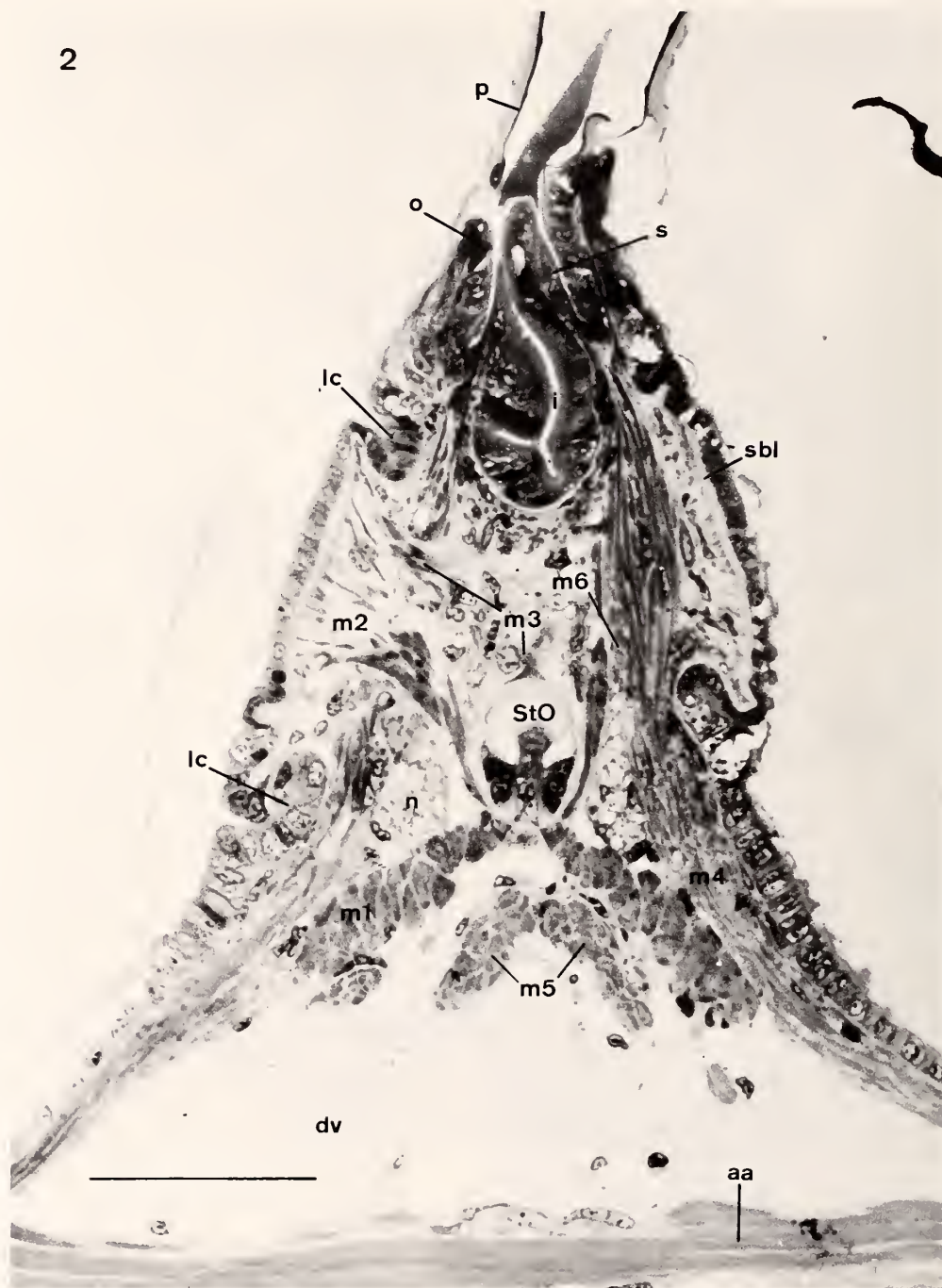


Figure 2

Nucula nucleus. Cross section of the dorsal mantle at middle zone of Stempel's Organ. aa, anterior adductor; dv, dorsal blood vessel; i, inner fold of mantle margin; lc, longitudinal clefts; m1, 2, 3, 4, 5, 6—muscles m1, m2, m3, m4, m5, m6; n, nerve of StO; o, outer fold of mantle margin; p, periostacum; s, sensory fold of mantle margin; sbl, specialized basal lamina (attachment zone of m2 and m3); StO, Stempel's Organ. Scale bar: 50 μ m.

between the anterior adductor and the first pedal retractor, and then forward beneath the StO dorsal to the anterior adductor (Figures 1b, 2). The nerve supplies the organ, especially in the anterior region, by several very thin neural fibers passing laterally through the basal lamina into the epithelium (Figure 4). After passing the anterior end of the StO the nerve runs into the anterior mantle margin.

Mantle epithelium: Three folds of the mantle margin can be distinguished in the region of the StO (Figures 2, 8): The inner fold (i) forms a cleft anteriorly, but changes gradually into a strong central fold at the middle region of the StO; the sensory fold (s) is very small and there are no special sensory elements in this region; the outer fold (o) produces the periostracum at its inner side.

Laterally in the mantle epithelium there appear two longitudinal clefts (lc) limiting the insertions of muscles m2 and m3 (see below). Ventral to this zone there are no special features until the attachment area of the anterior adductor begins.

Muscle system: Several special muscles are found near the StO and three of them (paired) are attached to its basal lamina:

The thickest of these muscles (m1) is attached to the StO at its ventral side. The muscle runs obliquely forward and is attached to the shell immediately anterodorsally to the anterior adductor (Figure 1b). The attachment epithelium consists of very flat ($1\text{--}2\text{ }\mu\text{m}$ high) cells containing many bundles of microfilaments. It is similar to the attachment epithelium of the anterior adductor, which is higher ($2\text{--}3\text{ }\mu\text{m}$), but nearly lacks nuclei (Figure 16).

A second pair of muscles (m2) is attached to the StO immediately dorsal to m1. The muscles m2 turn dorsally and laterally and are attached to the epithelium of the mantle (Figure 2). The attachment epithelium of these muscles (m2) is characterized by an extremely thick ($2.5\text{--}3\text{ }\mu\text{m}$) basal lamina that is divided by a very thin electron-dense membrane into two layers (Figure 17). The muscle fibers penetrate the lower layer only and are attached by an electron-dense vesicle. The epithelium itself consists of two cell types, one with electron-dense cytoplasm and few microfilaments (x), the other with a more electron-lucent cytoplasm (y).

The third pair of muscles (m3) is attached dorsally to the StO. The muscles m3 cross each other (Figures 2, 3, 5) and run sideways to reach the mantle epithelium immediately dorsal to muscle m2. Their attachment epithelium is elaborated in the same way as described above for muscle m2 (Figure 17).

Along the whole length of the StO, the mantle is coated on the inside by a substantial muscle (m4), extending from the outside of the inner cleft (i) of the mantle margin ventrally (Figures 2, 9). It is attached to the shell dorsal to muscle m1 (or dorsal to the anterior adductor in the posterior region). The attachment epithelium of this muscle looks like that of muscle m1.

Two pairs of longitudinal muscles (m5 and m6) are found near the StO, reaching into the dorsal mantle process up to the hinge, where they are fused and attached to the shell. The larger pair (m5) is located ventral to muscle m1; the smaller pair (m6) is found lateral to the StO, immediately above the nerve (n) (Figures 2, 3, 8).

Structure of Stempell's Organ

General organization: Stempell's Organ forms a narrow tube that is closed at both ends and thus lacks direct contact with the external water. In general the lumen of the organ is not placed centrally, but is shifted dorsally by a thickened ventral epithelium. The lumen is additionally narrowed by a high, longitudinal, ventral crest whose cilia fill it almost entirely.

In the following, the structure of the StO as a whole is described at five positions (a–e) from the anterior to the posterior end (Figures 4–8). All measurements are for adult specimens.

(a) A short distance behind the anterior end a cross section of the StO is circular, with a diameter of $60\text{ }\mu\text{m}$. The dorsal epithelium is very flat ($1\text{--}2\text{ }\mu\text{m}$), extending $15\text{ }\mu\text{m}$ ventrally, and the crest is $25\text{ }\mu\text{m}$ high (Figure 4). A special central zone is not elaborated, but most of the innervation is in this region.

(b) From a short distance behind the anterior bulb to the posterior quarter the StO has the following organization. The diameter is smaller ($50 \times 30\text{ }\mu\text{m}$), and the extremely flat dorsal epithelium lacks nuclei. A special tissue, forming "longitudinal septa" (see below), separates a central zone below the crest which is narrower in this region (Figures 2, 3, 5).

(c) In the last quarter of the StO its diameter increases, the dorsal epithelium is thickened to $8\text{ }\mu\text{m}$, and it contains nuclei (Figure 6).

(d) The crest flattens toward the end of the organ, then disappears together with the central zone (Figure 7).

(e) Finally the lumen disappears. There is no posterior bulb in *Nucula nucleus* and *N. sulcata* as figured by DREW (1901) for *N. delphinodonta* (Figure 8).

Structure of the non-specialized epithelium: Although the height of the epithelium lining the lumen of the StO varies greatly, its structure does not change. All cells have more or less round nuclei and bear a microvillous border, but otherwise there are no special features. Anteriorly some nervous tissue is found at the bases of the cells, running from the place of innervation (always lateral) downward into the central zone, penetrating the "longitudinal septa."

The basal lamina of the StO is thick ($2\text{--}3\text{ }\mu\text{m}$). This seems to be necessary for the attachment of the muscles, which are fixed to the lamina by prominent toothlike projections (especially m1, see Figure 3). Laterally the basal lamina is penetrated by the thin neural fibers emerging from the laterally placed nerves (Figure 4).

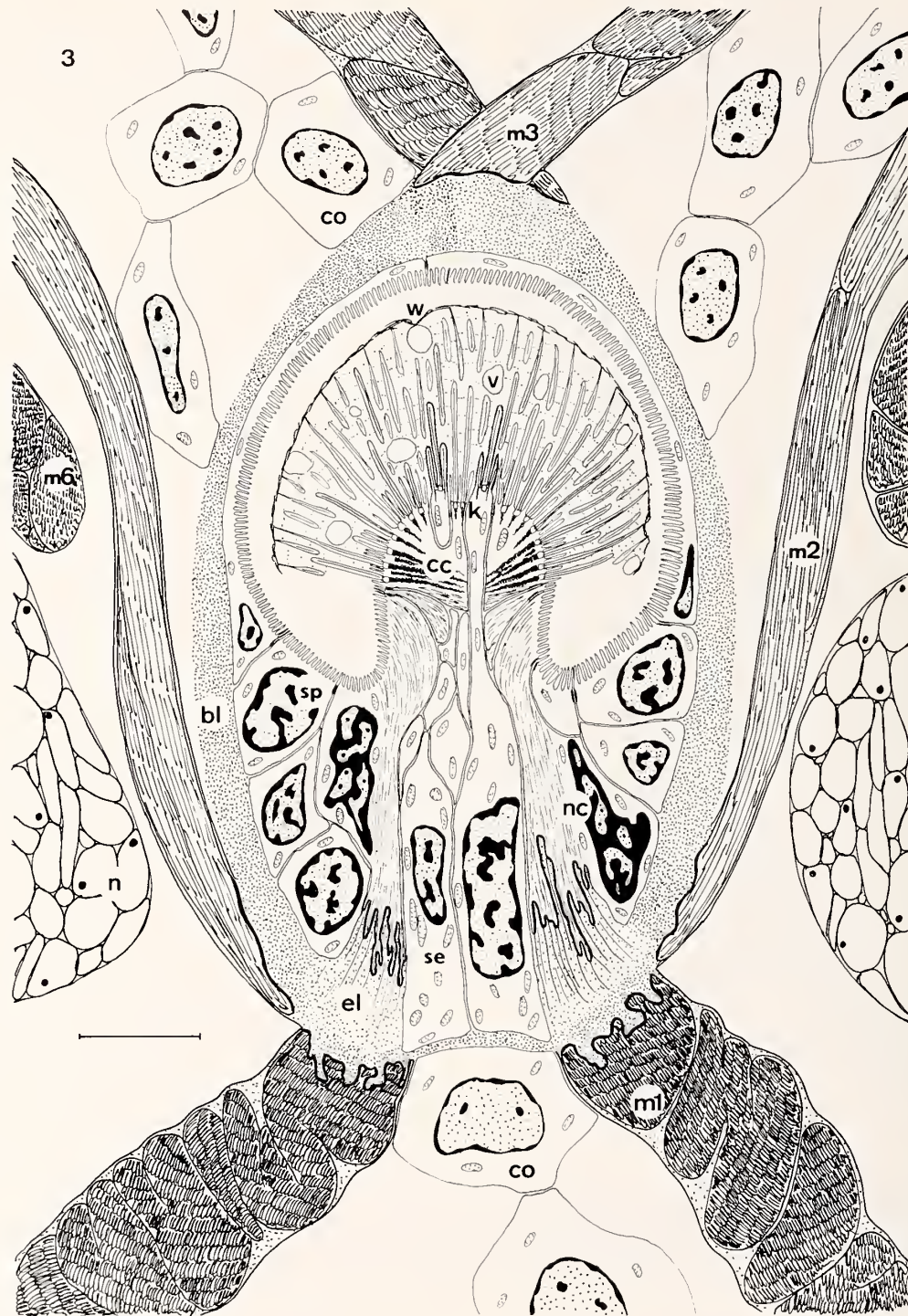


Figure 3

Nucula nucleus. Cross section of middle zone of Stempell's Organ (semischematic). bl, basal lamina; cc, ciliated cell; co, connective tissue; el, elastic layer (a specialized portion of the basal lamina); k, sensory knob; m1, 2, 3, 6—muscle m1, m2, m3, m6; n, nerve of StO; se, sensory cell; sp, supporting cell; nc, neighboring cell (with a specialized portion); v, vesicle; w, wrapper. Scale bar: 5 μ m.

Structure of the “longitudinal septa”: The symmetrically placed longitudinal septa separate a central zone in the ventral area of the lining epithelium. These septa are located exactly above the place of attachment of the thick oblique muscle m1. They consist of two portions (Figures 3, 15): (a) Ventrally a specialized region (el) of the basal lamina, conical in cross section, contains numerous thin microfilaments. (b) This region is continued upward by muscular portions of the laterally adjacent cells (nc) entering the crest and forming its lateral basis. The attachment to the lower portion of the longitudinal septa is by numerous rootlike projections which are invested with electron-dense material. The nuclei of the adjacent cells are slightly different from those of the non-specialized epithelium, having a more oval shape and bigger granules (150–200 nm) within their reduced euchromatin.

Structure of the central zone and of the crest: The central zone consists of large cells with oval nuclei. The cytoplasm of these cells is granular and more electron-lucent than that of the supporting cells (Figures 3, 15). They project slender (1 μm) processes up to the median surface of the crest. There, these processes form a kind of knob (2–3 μm), being somewhat higher than the surrounding ciliated cells (cc). The processes are arranged in transverse rows (Figure 14). At the anterior end of the StO up to seven processes are found within a row; going backward this number is gradually reduced to two. Each of the knobs bears a so-called collar receptor, consisting

of a specialized cilium that is surrounded by nine specialized microvilli (=“stereo-cilia” of many authors) (Figure 12). These cilia lack striped roots, have an thickened outer membrane, and are somewhat stouter (280–300 nm) than the cilia of the ciliated cells (200–230 nm). The structure of the collar cilia is likewise distinctive, showing a 9×3 pattern of outer microtubules and an electron-dense circle around the central tubules up to their tips (Figure 12). The basal body of the cilium forms a starlike plate from which several rootlets (not striped) run downward (Figure 13). The microvilli are triangularly shaped in cross section with amplified tips toward the central cilium. They are connected by a dense glycocalix forming a kind of fence around the central cilium.

Between the rows of processes and surrounding them, ciliated cells (cc) form the bulk of the crest. The whole breadth of the crest is always occupied by a single ciliated cell which obviously lacks a nucleus. The ciliated cells bear many cilia, but only few mitochondria are found. Whereas the more dorsally placed cilia have short roots, those of the more laterally placed cilia are very long and cross each other at the center of the crest (Figures 3, 14). Since these roots are alternately arranged with the rows of processes, a striped pattern is found in oblique sections of the crest (Figures 4, 14). The cilia of the ciliated cells are connected one to another by a net of glycocalix (Figures 3, 10, 11, 14) and so form a kind of matrix. In contrast to the shafts of the cilia, which are of normal structure, the microtubule pattern is progressively dis-

Explanation of Figures 4 to 13

Nucula nucleus. Figures 4 to 7. Cross sections of Stempell's Organ at different zones of the organ. Scale bars: 10 μm .

Figure 4. Immediately behind the anterior end (arrow: innervation).

Figure 5. Middle zone (for details see Figure 3).

Figure 6. Posterior quarter.

Figure 7. Near the posterior end.

Figure 8. Cross section of the dorsal mantle process at the first anterior hinge-tooth (immediately before the posterior end of Stempell's Organ). Scale bar: 50 μm .

Figure 9. Detail of Figure 2 to demonstrate the secretion of hypostracum material (decalcified). Scale bar: 10 μm .

Figures 10 to 13. Specialized cilia of Stempell's Organ; all cross sections are slightly oblique and are centripetally arranged. Scale bars: 200 nm.

Figure 10. Spearlike tips of supporting cilia together with the netlike wrapper.

Figure 11. Supporting cilia connected by glycocalix.

Figure 12. Typical collar receptors.

Figure 13. Bases of collar receptors.

h, hypostracum; i, inner fold of mantle margin; lc, longitudinal cleft; m(5+6), fused muscles m5 and m6; o, outer fold of mantle margin; p, periostracum; s, sensory fold of mantle margin; StO, Stempell's Organ.

Explanation of Figures 14 to 17

Nucula nucleus. Figure 14. Oblique section of the crest of Stempell's Organ immediately behind the anterior end.

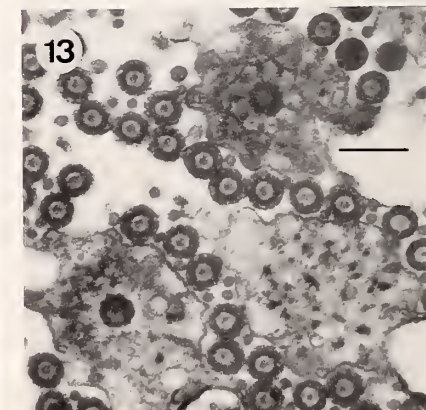
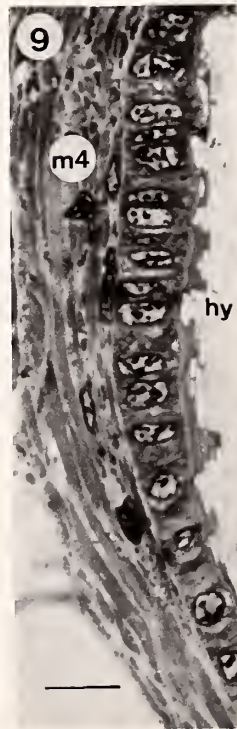
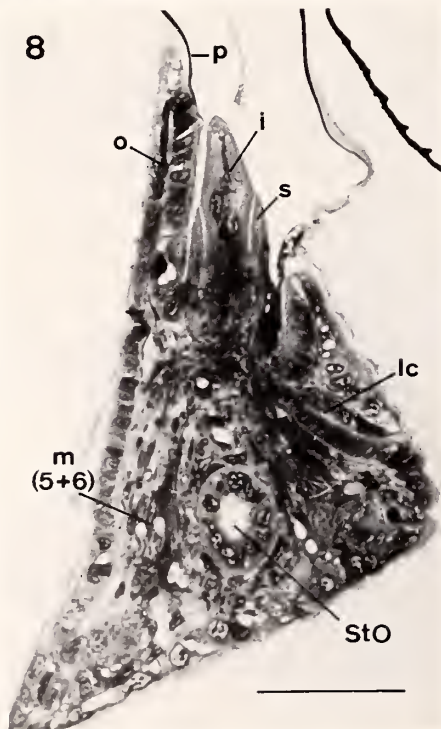
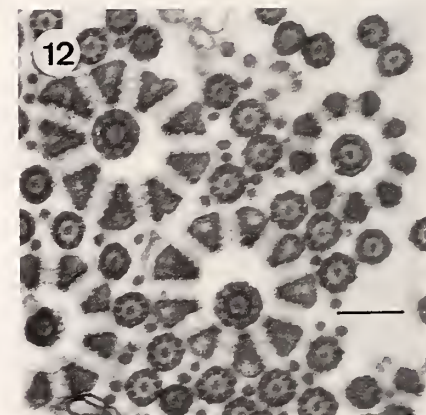
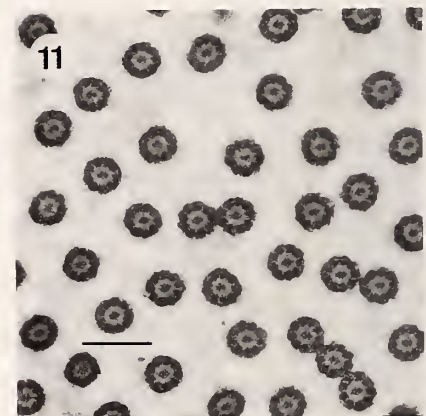
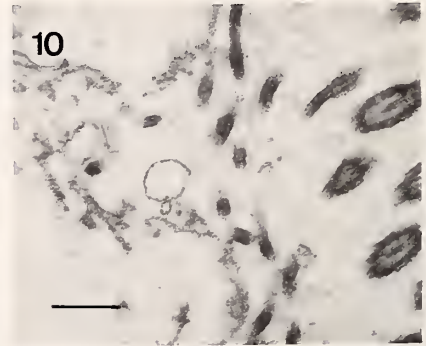
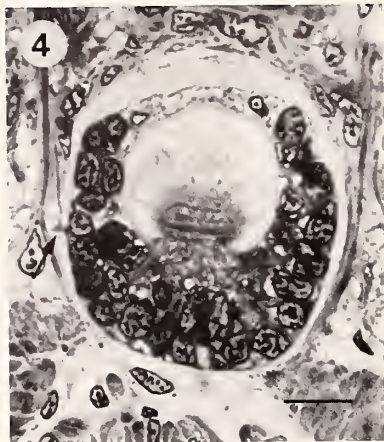
Figure 15. Cross section of the central zone and the longitudinal septa of Stempell's Organ near middle zone (see also Figure 3).

Figure 16. Attachment epithelium of the anterior adductor.

Figure 17. Attachment epithelium of muscle m2.

at, adhesive tissue; bl, basal lamina; cc, ciliated cell; cr, collar

receptor; ct, connective tissue; el, elastic layer (a specialized portion of the basal lamina); ibl, inner layer of basal lamina; hy, hypostracum; k, sensory knob; mf, muscle fibrils; nc, neighboring cell; obl, outer layer of basal lamina; se, sensory cell; sp, supporting cell; v, vesicle; w, wrapper; x and y, cell types x and y (see text). All scale bars: 2 μm .



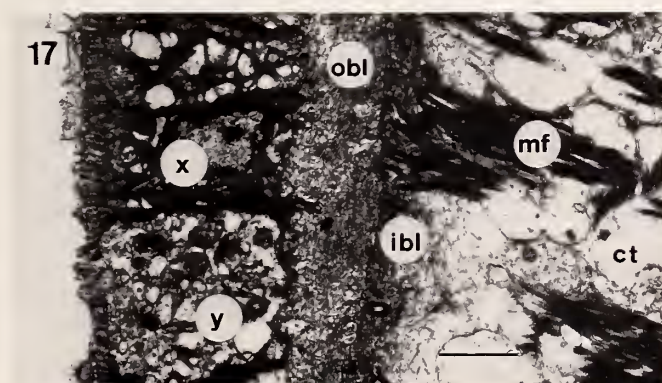
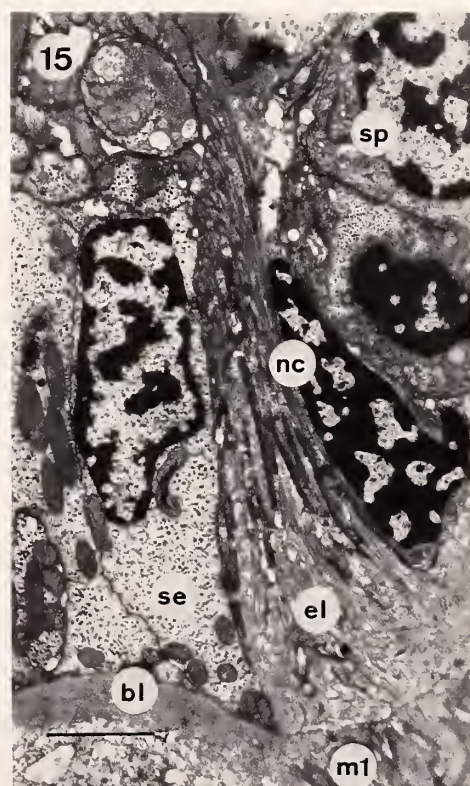
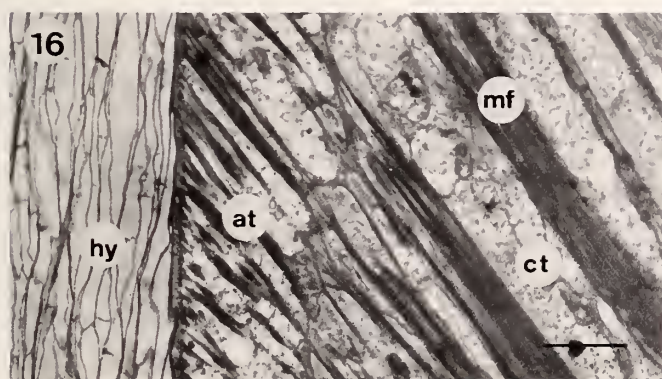
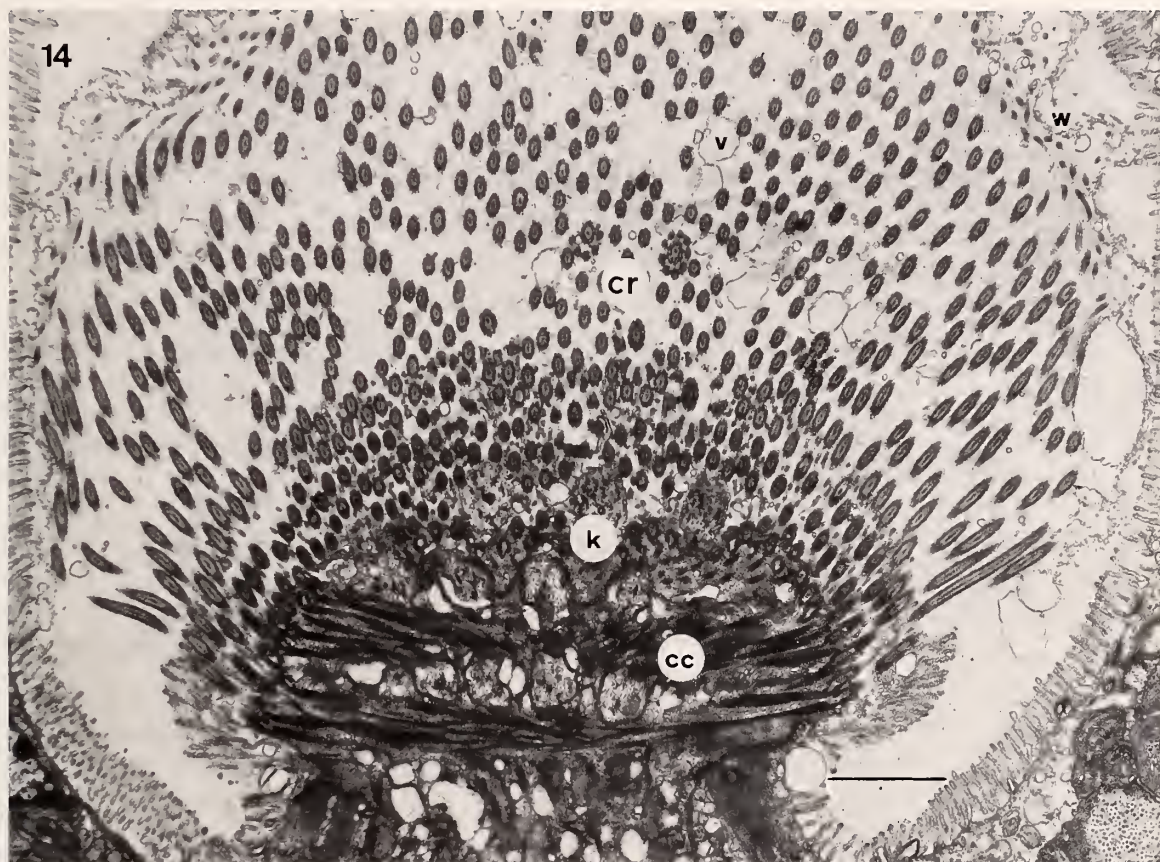


Table 1
Comparison of well investigated molluscan sense organs with collar receptors.

Organ	Stempell's organ	Abdominal sense organ	Long mantle tentacles	Epipodial sense organ	Subpallial sensory strip
Found in	<i>Nucula</i> (Nuculidae?)	<i>Pteriomorpha</i> and <i>Neotrigonia</i>	<i>Placopecten</i> (Pectinoidea?)	Vetigastropoda ¹	Docoglossa
Number per specimen	one	one or two	numerous	two to numerous	two
Position	dorsal to the anterior adductor	ventral to the posterior adductor (inside or outside of ctenidia)	mantle margin	ventral bases of epipodial tentacles	around the anterior edge of the shell muscles, subpallial
Innervation	cerebral	visceral	visceral	pedal	pleural (and osphradial?)
Contact with medium	no contact (closed tube)	contact with water of the mantle cavity	contact with external water	contact with external water	contact with water of the subpallial cavity
Basis of collar receptor	slightly higher than adjacent cells	same height as adjacent cells	forming a papilla together with adjacent cells	deeper than adjacent cells	slightly higher than adjacent cells
Central cilium of collar receptor	short (up to 5 μ m); lacking roots and basal foot specialized structure	very long (up to 500 μ m); with long roots and basal foot; normal structure; sometimes swollen membranes	short (up to 5 μ m); with long roots and basal foot; normal structure	variable (4 to 80 μ m); lacking root and basal foot; less specialized structure; accessory centriole	variable (2 to 15 μ m); with root and basal foot; normal structure
Specialized microvilli ("stereo-cilia")	nine; triangular in cross section; lacking rootlets	nine; round in cross section; with rootlets	eight (?); round in cross section; lacking rootlets	eight or nine; triangular in cross section; lacking rootlets	nine; round in cross section; with rootlets
Suggested primary function	mechanoreceptor	mechanoreceptor	mechanoreceptor	mechanoreceptor	mechanoreceptor
Suggested secondary function	reception of muscle contractions to regulate water currents and feeding movements	reception of pallial water currents to regulate them	reception of touch	reception of touch stimuli from the bottom (in connection with epipodial tentacles)	reception of subpallial water currents to regulate them
References	this paper	MOIR, 1977a; ZHADAN & SEMEN'KOV, 1982; HASZPRUNAR, 1985	MOIR, 1977b	MACDONALD & MAINO, 1964; CRISP, 1981; Haszprunar unpubl.	STÜTZEL, 1984; HASZPRUNAR, 1984

¹ According to SALVINI-PLAWEN (1980): zeugobranchs and trochoids.

solved near the tip of the cilium. The tip itself is spearlike and contains a single tubule only. Since the tips are found bent (Figure 10, 14), they appear to be flexible. Between the cilia, vesicles (v) of various diameters (0.5–2 μm) are found that are probably transported up to the tips of the cilia. There the vesicles form a netlike wrapper enveloping the whole crest complex (Figures 3, 10, 14).

DISCUSSION

On the Structure of the Receptor Elements

There can be little doubt that the so-called collar receptors found in the crest are sensory structures. This is shown not only by their specialized structure, but also by the fact that the presumed sensory cells, which bear these receptors, are in synaptic contact with the fine nervous fibers emerging from the lateral nerve.

Such collar receptors are found in many invertebrate groups, but appear to be often confused by authors with the so-called choanocyte-like cells (e.g., CRISP, 1981). Choanocyte-like cells are not sensory and lack the special features of the central cilium as well as of the surrounding microvilli. Within the Turbellaria collar receptors are found in the integument of nearly all groups, and structural differences are used for phylogenetic suggestions (e.g., EHLERS, 1977; EHLERS & EHLERS, 1977; SOPOTT-EHLERS, 1984).

Within the Mollusca, collar receptors are found so far in very different organs: they occur (a) in the subpallial sensory stripe of the Docoglossa (STÜTZEL, 1984; HASZPRUNAR, 1984); (b) in the epipodial sense organs of Vetigastropoda² (CRISP, 1981; Haszprunar, unpublished); (c) at the mantle slit (or siphon) of fissurellids (Herbert, personal communication); (d) at the ventral mantle margin of the pteropod *Creseis virgula* (Haszprunar, unpublished); (e) in the abdominal sense organs of Pteriomorpha (MOIR, 1977a; HASZPRUNAR, 1985); (f) at the long mantle tentacles of the scallop *Placopecten magellanicus* (MOIR, 1977b); and (g) in Stempell's Organ of *Nucula* (this paper).

Although the organs of the various classes and tribes, where collar receptors occur, are certainly not homologous, it seems hardly likely that such a complex structure would have evolved independently in each case. However, as outlined in the cases within the Mollusca, which have been investigated in detail, there are several differences in the detailed structure of the collar receptors of the respective organs (Table 1). Thus, two possibilities remain: (i) the collar receptors of different organs are the products of convergence, independently developed from a choanocyte-like cell, or (ii) there is a common basal genetic information to develop an archetype of these receptors, which have been secondarily specialized for the special function of the particular sense organ. This view is the theoretical

basis of all phylogenetic implications based on the structure of collar receptors within the Turbellaria (EHLERS, 1977). This would be a special kind of "normative" homology (e.g., RIEDL, 1975) which is normally restricted to single organelles only (e.g., mitochondria, cilia), or known as "serial" homology with respect to organs (e.g., ROTH, 1984).

In any case this type of receptor appears to be typical for mechanoreceptors (although there are many mechanoreceptors, such as statocysts, lacking collar receptors). In the case of the abdominal sense organ its suggested mechanoreceptive function (regulating water currents, see THIELE [1889], HASZPRUNAR [1985]) has been recently confirmed by electrophysiological results (ZHADAN & SEMEN'KOV, 1982). Further, a chemo- or osmosensitive StO is very improbable, since the organ has no contact with external water, being closed.

Therefore, it is very probable that the StO is a mechanoreceptor.

On the Structure of the Supporting Elements

The well-developed roots found in the ciliary cells indicate a high mechanical stress on their cilia (especially the laterally located ones). In contrast, several structural facts indicate that these cilia do not move, but form a kind of elastic matrix covered by the netlike wrapper: (i) the presence of few mitochondria in the ciliated cells (Figure 14); (ii) the connection of the cilia among each other by a glyocalix (Figure 11); (iii) the spearlike tips of the cilia which appear to be flexible (Figures 10, 14). It follows that there is a passive mechanical stress on these cilia.

In fact, a highly developed structure to transmit mechanical forces from outside to the crest is found in the paired longitudinal septa, immediately situated above the place of attachment of muscle m1. Any contraction of this muscle is transmitted via the specialized basal lamina and via the muscular portion of the adjacent cell to the lateral basis of the crest (Figures 3, 15).

Comparing the three muscles attached to the StO, the following main differences between muscles m2 and m3 and muscle m1 are found. The former muscles are symmetrically arranged with respect to the longitudinal axis of the StO. Their mode of attachment at the lateral mantle epithelium by a thickened basal lamina (Figure 17) does not allow extreme mechanical stress. In addition, there are no special structures to transmit contractions of these muscles into the StO, and their attachment zone on the StO is not toothlike (as for muscle m1), likewise indicating a low degree of mechanical stress. Thus, it is probable that the muscles m2 and m3 are necessary for the stability of the StO, but do not act in the reception process. In contrast, muscle m1, which is the thickest, runs obliquely forward and this appears to be correlated (a) with the presence of the majority of the collar receptors at the anterior end of the StO, and (b) with the fact that penetrating neural fibers likewise are found only in the anterior

² After SALVINI-PLAWEN (1980): zeugobranchs and trochoids.

third of the organ. In addition, the muscle is directly attached to the shell via a special attachment tissue similar to that of the adductor muscle (Figure 16), and its contractions can be transmitted by the longitudinal septum.

On the Function of the StO

Summing up the considerations presented so far, it can be concluded that the StO is a mechanoreceptor, detecting contractions of muscle m1.

To date, a StO has been found only within the genus *Nucula*, but is likely present also in other genera of the Nuculidae (Nuculoidea). Because the discoverer of the StO did not describe a similar structure in any of the members of the Nuculanoidea and Solemyoidea he investigated (STEMPELL, 1898, 1899; DREW, 1899), the StO appears to be restricted to the Nuculidae.

The Nuculidae is the sole family among all Bivalvia which has retained an anterior-posterior water current (similar conditions found in the Lucinoidea are accepted by most authors to be secondary, see *e.g.*, ALLEN [1958], MORTON [1979]). STASEK (1961) stated that feeding in nuculids is done (a) by the palp proboscides (as in all protobranchs), (b) by the outer palp lamellae (only nuculids in such a degree), and (c) by the ctenidia (less important in nuculids). Thus, the incoming water is used not only for respiration, but also for feeding. Reflecting that the adhesive zone of muscle m1 is located immediately dorsal to the anterior adductor and thus exactly beside the inhalant opening of the water current (Figure 1b), it appears probable that the StO detects movements (also longitudinal) of this important region, where disturbances are essential for two main life processes.

Therefore, the presence of the StO within the Nuculidae is additional evidence for the ideas of STASEK (1961) that nuculids are not direct forerunners of higher Bivalvia. They represent an early offshoot of the bivalve stock, specialized in a considerable degree. The StO represents one example of this specialization.

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LITERATURE CITED

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